An enigmatic rock-dwelling land snail from southernmost Iberia (Mollusca, Gastropoda, Helicidae)

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http://zoobank.org/References/7dab39f0-43d3-4804-976c-71a1de49f801

Abstract - A new species and genus of helicid land snail, *Tartessiberus cilbanus*, is herein described from the extreme south of continental Spain. In spite of being fairly large and conspicuous, it has hitherto remained unknown due to its highly restricted ecological and geographic range –it is apparently restricted to the core of Serranía de Grazalema, an elevated karstic area receiving the highest rainfall in all of Iberia because of its location in proximity to the Strait of Gibraltar. The genital anatomy of the new species indicates it belongs within the tribe Allognathini, but it remains unclear whether it is closer to the southeastern Iberian endemic *Iberus*, or to *Allognathus* from the Balearic Islands. Its radula and shell are reminiscent of the latter, but this might be a case of convergence on crevice dwelling and feeding on bare rock surfaces. This rare, restricted-range endemic deserves conservation attention.

Keywords - Endemism, karst, Grazalema, Andalusia, Allognathini, genitalia, rock-scrapping radula.

Resumen - Se describe una nuevo género y especie de caracol terrestre helícido, *Tartessiberus cilbanus*, del extremo meridional de España continental. A pesar de ser bastante grande y llamativo, ha permanecido desconocido hasta ahora debido a su limitada distribucion ecológica y geográfica; parece restringido al núcleo de la Serranía de Grazalema, un macizo cárstico que recibe la mayor pluviosidad de toda Iberia como consecuencia de su proximidad al Estrecho de Gibraltar. La anatomía genital de la nueva especie indica que pertenece a la tribu Allognathini, pero no está claro si es más próxima a *Iberus*, endémico del sureste de la Península Ibérica, o bien a *Allognathus*, de las Islas Baleares. Su rádula y concha recuerdan las de este último, pero esto podría ser un caso de convergencia a habitar grietas y alimentarse en superficies rocosas desnudas. La conservación de este endemismo raro y circunscrito merece atención.

Palabras clave – Endemismo, carst, Grazalema, Andalucía, Allognathini, genitalia, rádula litoerosiva.

Introduction

During the last six years we have aimed at collecting and studying a puzzling land snail from southernmost Spain. It is herein described as a new species and genus. In spite of being fairly large and conspicuous, it has hitherto remained unknown due to its highly restricted ecological and geographic range.

Serranía de Grazalema is an elevated (1654 m) set of abrupt ranges at the limit between Cádiz and Málaga provinces, representing the wersternmost edge of the Subbetic Ranges. It receives the highest rainfall in all of Iberia, surpassing 2,400 mm annual mean in core areas, with years reaching over 3,200 mm. This is the combined effect of being located in proximity to the Strait of Gibraltar and standing as a major channel for humid winds (NARANJO-BAREA & *al*., 2017). The local climate is typically Mediterranean, with a long, dry summer with temperatures above 20 ºC, and a cool (below 10 ºC) rainy winter. Such extreme climate has produced an impressive karst geomorphology, mostly on Jurassic limestones, exarcerbated by glacial processes and more recently deforestation (DELANNOY, 1998).

This unique setting harbors a highly endemic biota (BEL ORTEGA & APARICIO GARCÍA, 1989). It is a unique biogeographic enclave, encompassing less than 1% of Andalusia (DOMÍNGUEZ VILCHES, 1988). It belongs into the Rondense district, which constitutes the westernmost edge of the mountains included in the Mediterranean-Ibero-Atlantic region (RIVAS-MARTÍNEZ & *al*., 1997; Mota & al., 2002).

The Iberian endemic genus *Iberus* Montfort, 1810 includes an uncertain number of species, yet it is clearly diversified in the Betic area of southeastern Iberia (Rossmässler, 1854-1859; Schmidt, 1855; García San Nicolás, 1957; Cobos, 1980; Elejalde & *al*., 2008a,b; Schileyko, 2006; Welter-Schultes, 2012). It belongs within the Allognathini, a small tribe of helicines (Kneubühler & *al*. 2019; Holyoak & *al*., 2020) including the well-known *Cepaea* Held, 1838 and *Caucasotachea* Boettger 1909, the Western Mediterranean *Pseudotachea* Boettger, 1909, and also two genera endemic to the Balearic Islands, *Allognathus* Pilsbry, 1888 and *Iberellus* Hesse, 1908. The latter two genera have been considered synonymous, but we refuse such proposal on the basis of the striking anatomical and ecological differences separating them (Altaba, 1991 ; Welter-Schultes, 2012).

The Western Mediterranean region is a dynamic biogeographic setting; in spite of common misinterpretations, both vicariance and dispersal have played important roles in shaping the distributions of endemic taxa (Altaba, 1998, 2014, 2021). Our finding of a hitherto unknown species of allognathine in Serranía de Grazalema, obviously well adapted to local rocky habitats, poses a number of phylogenetic and biogeographical questions, as it shares traits and ecology with both the continental *Iberus* and the insular *Allognathus*.

Material and methods

Collecting in Serranía de Grazalema was performed by FRJ repeatedly, with special emphasis on karstic formations. Live specimens were found aestivating in crevices, or active after heavy rains. They were observed and photographed, and then drowned and preserved in 80% ethanol.

Dissections were performed by CRA under an Olympus SZ-30 dissecting microscope, with the aid of fine, sharpened twizzers, iridectomy scissors and entomological pins. The radula, jaw and dart were extracted, prepared and mounted, and observed under a Leica DME compound microscope. Drawings were prepared on the basis of various photographs and direct observation.

The following measures were taken on shells (as defined by Breure & Vega-Luz, 2020): height (H), width (W), aperture height (AH), aperture width (AW), last whorl height (LW), number of whorls (NW).

Anatomical terminology follows Giusti & *al*. (1995). Abbreviations used in figures are as follows:

AG: albumen gland
AP: annular pad
BC: bursa copulatrix
BCD: diverticulum of bursa copulatrix
BW: body wall
CD: copulatory duct
CLS: crest-like structure
DBC: duct of bursa copulatrix
DDP: distal cavity of distal penis
DE: distal epiphallus
DG: digitiform glands
DP: distal penis
DS: dart sac
DV: distal vagina
E: epiphallus
F: flagellum
FHD: first hermaphrodite duct
FO: free oviduct
G: glans of penial papilla
GA: genital atrium
PDP: proximal cavity of distal penis
PE: proximal epiphallus
PPDP: papilla in the proximal cavity of the distal penis
PI: pilaster
POS: prostatic ovispermiduct
PP: proximal penis
PR: penial retractor muscle
PS: penial sheath
PV: proximal vagina
PW: penial wall
T: talon
UOS: uterine ovispermiduct
VD: vas deferens

The material on which this study is based has been deposited in the following collections: Museographic Collection of the first author (CRA), Sociedad Gaditana de Historia Natural (SGHN), Museu Balear de Ciències naturals (MBCN), Muséum d'Histoire Naturelle de Genève (MHNG).

Systematics

Family Helicidae Rafinesque, 1815

Subfamily Helicinae Rafinesque, 1815

Tribe Allognathini Westerlund, 1903

Tartessiberus gen. nov.

http://zoobank.org/NomenclaturalActs/625e223a-28bf-4ae2-90c0-7b4d3b179f3e

Diagnosis.- Mid-sized helicines with thin semiglobose shell, rock-scrapping radula, stout ridged mandible, exceedingly long flagellum and diverticulum of bursa copulatrix, proximal cavity of distal penis limited by two medial papillae and having a small papilla on the inner wall, crest-like structure at distal end of penis, and four-edged spear-shaped dart with blades slightly enlarged near edge in the distal part.

Type species.- *Tartessiberus cilbanus* Altaba & Ríos, spec. nov.

Species included.- Monotypic.

Etymology.- A combination of *Iberus*, a closely related land snail genus that is endemic to the southeastern Iberian Peninsula, and the ancient Tartessian civilisation of southwestern Iberia. Gender masculine.

Tartessiberus cilbanus spec. nov.

http://zoobank.org/NomenclaturalActs/b075a355-5bb2-4ef3-a064-80055783443c

Diagnosis. - As for the genus.

Description.- Shell (**Fig. 1**) dextral, medium, thin, semiglobose, slightly depressed, broadly conical above and gently convex below, pale ochre with up to five thin chestnut bands that are very pale except for irregularly placed darker spots (the two intermediate bands may be obsolete); external surface opaque, with silky shine caused by a fine reticulate, dense sculpture made of colabral ridglets and very thin spiral lines, less marked on the lower surface; spire conical, low, with 3.9-4.2 slightly convex whorls, slowly and regularly growing except at the 1/4 whorl which becomes slighlty wider; last whorl large, noticeably depressed, well rounded at periphery and suddenly descending near apeture; suture shallow but incised; umbilicus completetely closed, covered by a thin, appressed expansion of the columellar callus; aperture oblique, nearly circular but narrowed towards columella, which is slightly thickened and forms a central small, tenuous tooth-like thickening; peristome widely interrupted, slightly thickened, shortly but noticeably reflected, whitish, with palatal edge regularly curved, joining columella with a very blunt angle but suddely twisted downwards just before ending on parietal surface.

Genitalia (**Fig**. **3**) with general structure typical of Helicidae (large, semidiaulic monotrematic). Genital atrium very short and narrow. Male branch relatively small, thin. Penis fairly long (2.5 times longer than epiphallus), slightly wider centrally. Epiphallus indistinct from proximal part of penis, moderately bulging near proximal end. Penial retractor muscle very short, connected to diaphragm. Flagellum exceedingly long (about 1.3 times the length of penis and epiphallus combined), thin at its apical half, which is rather rigid and regularly arching. Vas deferens moderatly long, narrowed at junction with epiphallus. Opening of vas deferens into epiphallus apically placed, small, surrounded by rosette-like pad. Penis divided internally into three distinct chambers (**Fig**. **4**). Proximal part (starting at attachment of penial retractor muscle) structurally continuous with epiphallus, sharing the thick simple wall and the four long, low anastomosing pleats along its inner surface; ending in small, conical glans of penial papilla with slightly lateral opening and thin walls. Distal part of penis with very thin external sheath throughout and internally medially-placed, well-developed annular pad giving rise to a moderately large conical structure with subterminal opening. Proximal part of distal penis (between glans and annular pad) with thickened muscular wall, especially distally where forming annular pad; internally with mucous epithelium forming transverse, densely pleated ridges, wider and taller at central region, gradually replaced by four strong muscular pilasters distally; a small papilla bulging from the wall near one third of length of cavity, ringed as a result of transverse ridges extending over it, formed as thickening of both the penial wall and mucous epithelium. Distal part of distal penis with thinner wall, internally with tenuous longitudinal pleats and a small but conspicuous, longitudnally oriented crest-like structure near opening into atrium.

Soft parts (**Fig.** 2) pale straw yellowish, with small, regularly spread tubercles on upper parts, becoming finer towards edge of sole and very fine on tentacles; slightly darker on head and neck; mantle border pale chestnut brown; sole undivided, pale greyish beige; wall of pallial cavity greyish brown with darker markings reproducing the color pattern of the translucid shell.

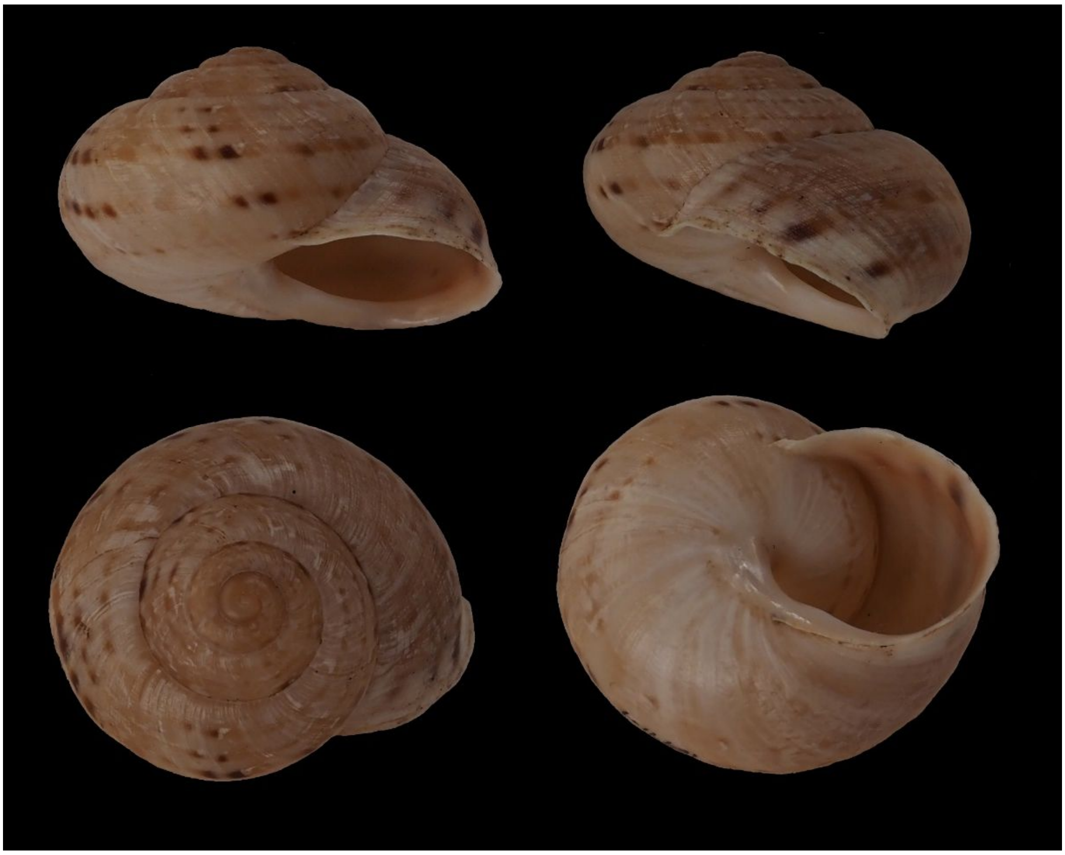


Fig. 1. Shell of holotype of *Tartessiberus cilbanus* gen. nov., spec. nov. Ø 27.3 mm.

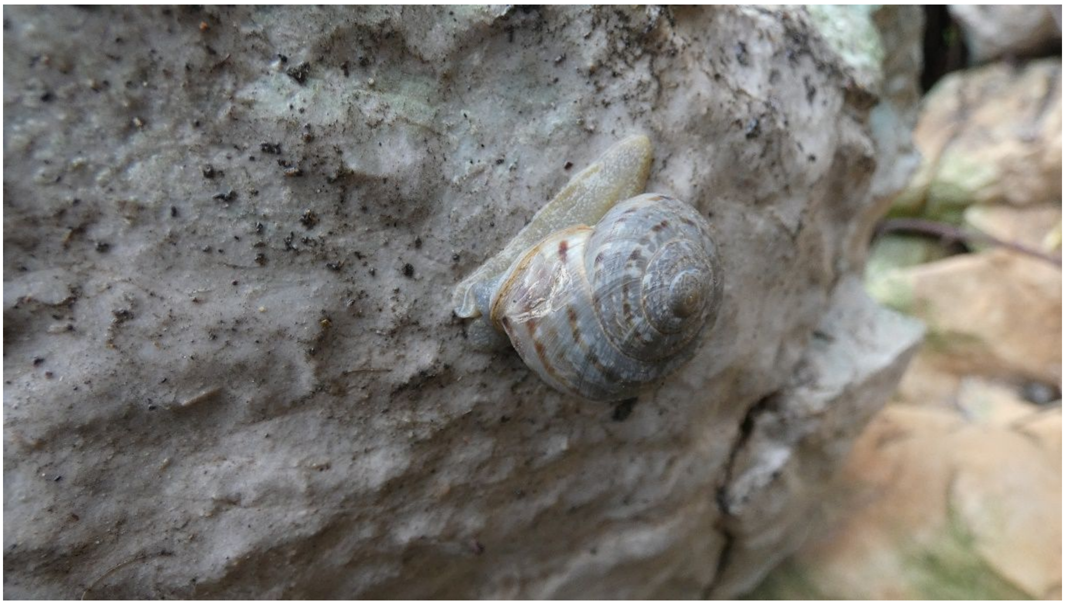


Fig. 2. Live specimen of *Tartessiberus cilbanus* crawling on bare rock surface after heavy rain.

Female branch robust and long. Dart sac broadly cylindrical, apically almost round, with very thick muscular walls, opening into distal end of vagina. Digitiform glands few, rather and slender, arising from two thin main trunks attched to distal vagina just above dart sac; each branch bilobed twicem thus giving rise to three thinner glands with slightly enlarged, club-shaped tips. Proximal vagina short, about length of distal part, narrowing distally. Duct of bursa copulatrix robust, basally thickened and narrowed apically, long (almost twice length of penis and epiphallus combined). Bursa copulatrix small, irregularly pear-shaped, its neck crossing diaphragm. Diverticulum of bursa copulatrix robust, dark greyish, extremely long (twice the length of duct of bursa copulatrix and copulatory duct combined). Free oviduct very short, as wide as proximal vagina. Prostatic ovispermiduct distinct, rather short, gradually and moderately enlarged proximally. Uterine ovispermiduct bulging, appressed to and somewhat longer than prostatic part, divided into a proximal pleated part and a distal inflated half. Albumen gland large (as long as oviduct and spermiduct combined), bulging near junction with ovispermiduct and grapually tapering towards its free end. First hermaphrodite duct robust, strongly pleated, narrow at tips and thickened centrally; at contact with albumen glands forms small talon.

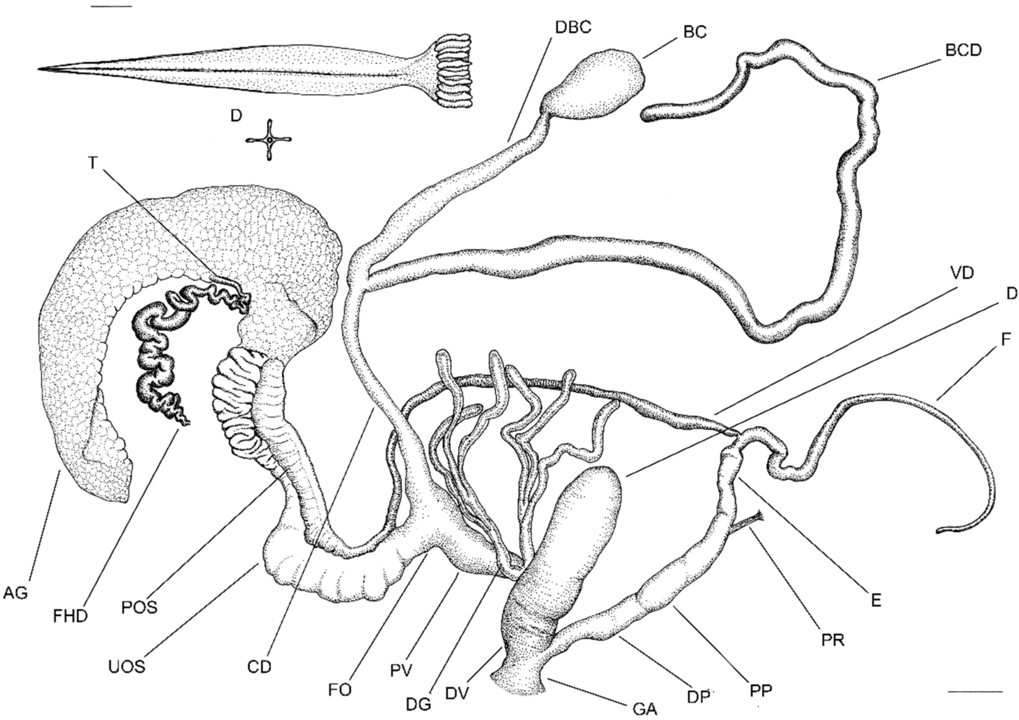


Fig. 3. Genitalia of *Tartessiberus cilbanus* gen. nov., spec. nov. (excluding gonad); scale bar = 2 mm. Upper left: the excised dart, together with a cross-section of its blade at mid-length; scale bar = 200 µm.

Dart spear-head shaped, rather narrow, more so apically, cylindrically hollow at its core, with four blades that are sharp proximally but apically become slightly enlarged near the edges; proximally the blades diminish gradually until disappearing, then core enlarged to become swollen base ending in crown of appressed leaflets.

Jaw (**Fig. 5**, bottom) odontognathous, rather short and stout, with five strong, rather irregular vertical ridges and three ill-limited concentric zones of decreasing thickness towards thin, irregular outline.

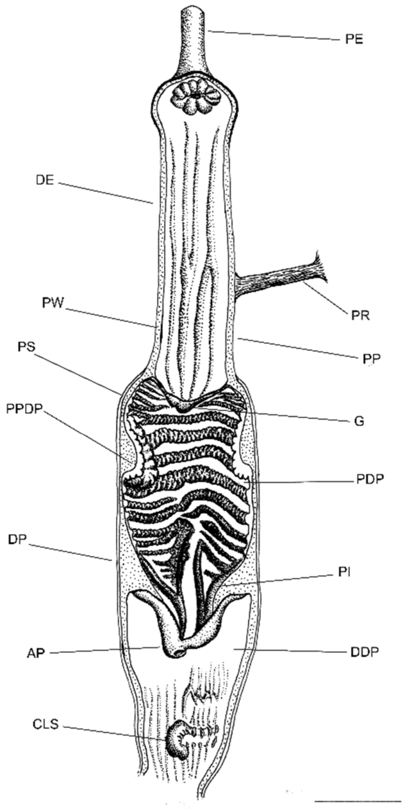
Radula (**Fig. 5**, top) with rows formed by 89 strong, broad dagger-like, imbricated teeth. Central tooth robust, with moderately wide basal plate and crown unicuspid; strong, thick single mesocone, sharp at point, gently curved inwards and heavily built. Laterals 13 on each side, similar in outline and structure, but slightly larger than central; very large medial cusp and very small ectocone on the marginal edge. Marginals 27 on each edge, smaller and more eccentric than laterals: base smaller, mesocone smaller and ectocone proportionately larger; progressively diminishing in size and split towards edge, the last 4 very small.

Type material. - Spain, Andalusia, Cádiz province, Serranía de Grazalema, Sierra del Endrinal, Cañada

Mahón, Peñón Grande, 36° 45’ 18,36” N; 5° 22’ 42,17” W, 1058 m, 12.x.2015. Holotype CRA-16941-1, and 3 paratypes (SGHN, MBCN and MHNG). Measurements of the material are given in Table 1.

	H	W	AH	AW	LW	NW
Holotype CRA	18.7	27.3	7.4	13.1	16.2	4.2
Paratype 1 SGHN	16.9	25.8	7.7	13.0	14.9	3.9
Paratype 2 MBCN	16.8	25.3	7.9	13.3	14.5	4.1
Paratype 3 MHNG	17.5	25.0	6.2	13.2	15.5	4.2

Table 1. Measurements (in mm) of shells of *Tartessiberus cilbanus* gen. nov., spec. nov.; for abbreviations see Methods.



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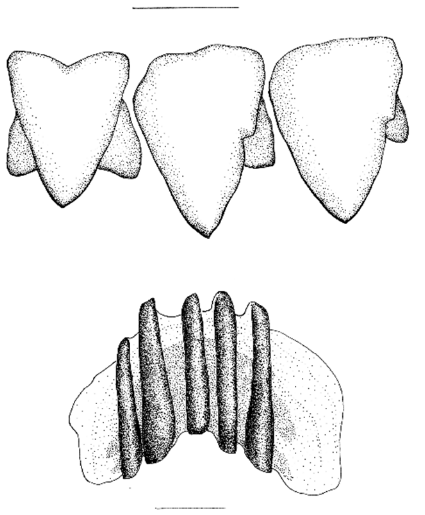

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Fig. 4. Internal structure of the penis in *Tartessiberus cilbanus* gen. nov., spec. nov. A longitudinal cut allowed nearly complete unfolding (except glans of penial papilla and annular pad, shown partially uncut). Scale bar = 2 mm.

Fig. 5. Radula and jaw of *Tartessiberus cilbanus* gen. nov., spec. nov. Top: only the central and first two lateral radular teeth are shown, set apart to show their shape without overlapping; scale bar = 25 µm. Bottom: excised jaw; scale bar = 200 µm.

Distribution.- In addition to the type locality, *Tartessiberus cilbanus* has been observed alive in several localities, all within the highest part of Serranía de Grazalema:

- ➢ Sierra del Caillo, 36° 41’ 49,61” N, 5° 23’ 18,70” W, 924 m, 12.x.2019, 5 specimens.
- ➢ Mirador del Cintillo, Sierra de Ubrique, 36° 40’ 56,82” N, 5° 25’ 21,91” W, 903 m, 12.x. 2019, 2 specimens.
- ➢ Sierra Peralto, 36° 41’ 08,61” N, 5°23’52,83” W, 1038 m, 7.xii.2019, 4 specimens.
- ➢ Villaluenga del Rosario, 36° 41’ 46,77” N, 5° 23’ 19,91” W, 905 m, 7.xii.2019, 5 specimens.
- ➢ Manga de Villaluenga, 36° 41’ 34,55” N, 5° 23’ 58,22” W, 999 m, 7.xii.2019, 5 specimens.

Habitat.- The new species lives in heavily karstified limestone areas (**Fig. 6**), always at high elevation (between 903 and 1058 m). If finds refuge during dry spells in deep crevices (**Fig. 7**), when it seals the aperture with a very strong, albeit thin epiphragm.

Etymology.- The species name is an adjective refering to the river Guadalete, known in Roman times as Cilbus and having its source in the new species' habitat.

Remarks.- The shell is reminiscent of a small *Iberus,* perhaps the wider forms of *I. loxanus* (Rossmässler, 1854). However, it can be readily distinguished by it lighter, more globose appearance and paler coloration. The very long appendices (flagellum and diverticulum of the bursa copulatrix), small papilla in the proximal cavity of the distal penis, robust radula with unicuspid mcentral tooth, and stout jaw also allow discrimination. The thin, subglobose shell and radula are similar to those of *Allognathus grateloupi* (Graells, 1846), although the latter is more globose, smaller, and with (usually) stronger dotted bands.

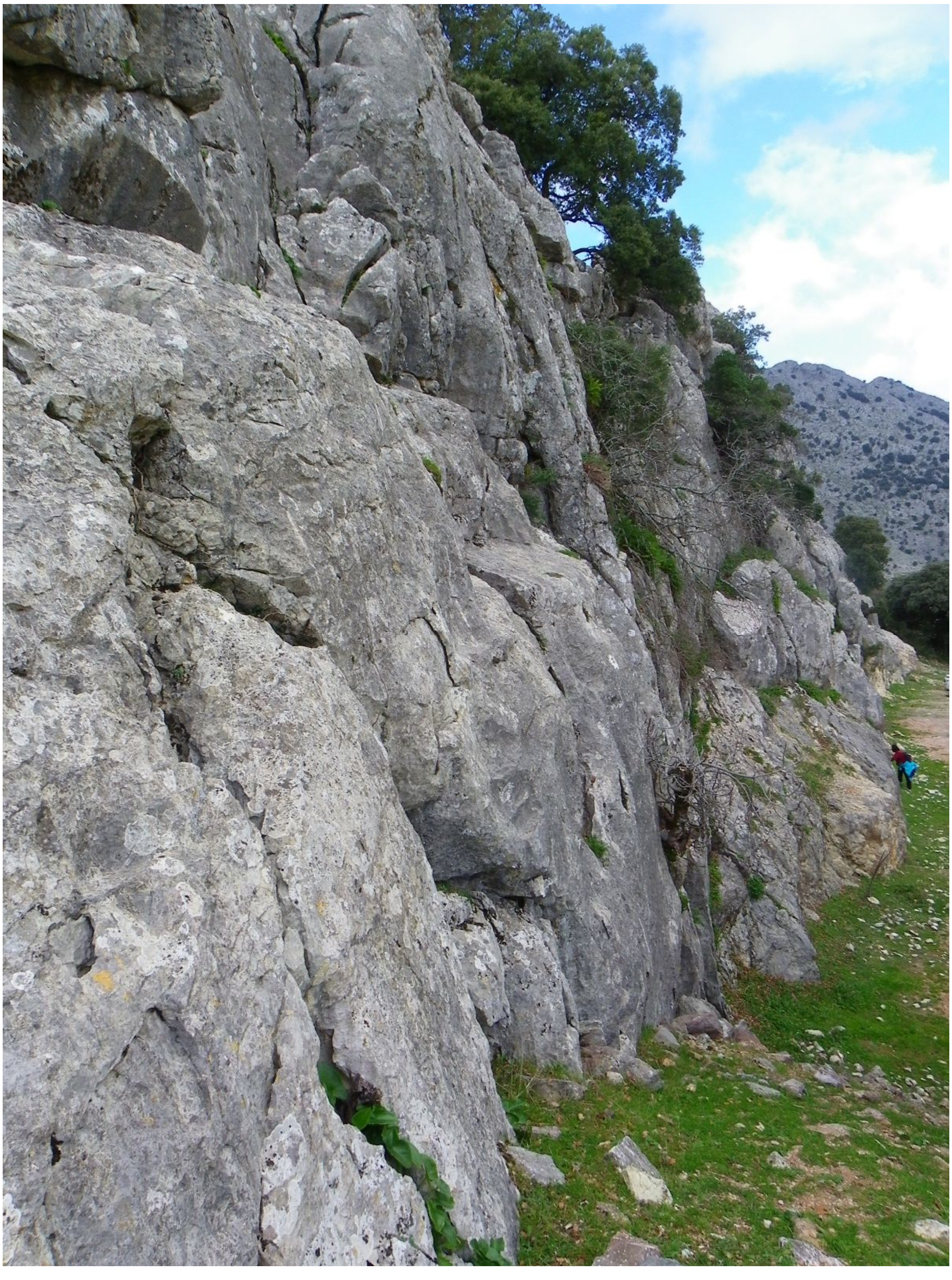

Fig. 6. Karstic habitat of *Tartessiberus cilbanus* gen. nov., spec. nov.

There is a need for caution when establishing homologies among internal features of the penis in Helicinae. The annular pad is most likely homologous with the distal penial papilla more robustly built in the Helicini tribe (NEUBERT & BANK, 2006). In allognathines, as well as in otalines (KNEUBÜHLER & *al*., 2019; HOLYOAK & *al*., 2020), this structure may be more or less developed, but is a functional, torus-like verge. However, the papilla in the wall of the proximal part of the distal penis of allognathines and otalines cannot be considered homologous with the proximal papilla surrounding the opening of the proximal penis in Helicini. Assuming the latter could shift laterally and modify its function is at the basis of a terminology involving proximal and distal penial papillae (NEUBERT & BANK, 2006) or P1 and P2 (KNEUBÜHLER & *al*., 2019). However, in *Tartessiberus* all three structures are present. We thus retain the nomenclature of GIUSTI & *al*. (1995:10) as valid and useful.

The remarkably stout structure of the radula in *Tartessiberus cilbanus* belongs to a peculiar type called "rock-scrapping radula", which occurs in phylogenetically unrelated land snails that feed by grazing bare rock surfaces (BREURE & GITTENBERGER, 1990). Thus, it is character state of questionable homology, even among closely related species.

Discussion

The unsuspected discovery of a fairly large land snail species and genus in Western Europe highlights the importance of natural history and taxonomic research as the fundamental basis for understanding and protecting biodiversity. Fortunately, the habitat of *Tartessiberus cilbanus* is totally included in the Sierra de Grazalema Natural Park. Nevertheless, focused ecological research and conservation action are needed, as is the case for rare endemic land snails (ALTABA, 2020).

Anatomical characters support a close relationship to other allognathines, especially *Iberus* and *Allognathus*. Unfortunately, at present there is a general lack of detailed, reliable anatomical data. Although similar to some of the smaller *Iberus*, the exceedingly long genital appendices, small penial lateral penial papilla and unique radula clearly seggregate *Tartessiberus*. Its rock-scrapping radula and semiglobose shell point at a relationship with *Allognathus*, but it is unclear whether this similarity is the outcome of convergence through adaptation to similar karstic habitats. The Serranía de Grazalema is an insular habitat for rock-dwelling land snails, so this possibly parallel evolution might be reinforced as an insularity syndrome (ALTABA, 2013). We have not detected any *Iberus* in this isolated high area, although this genus surely reaches mountain ranges located to the East and South. Research in progress, including both anatomical characters and molecular genetics, aims at elucidating the phylogenetic position and biogeographic history of *Tartessiberus*.

Acknowledgements

We are grateful to Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible, of the Junta de Andalucía, for issuing the collecting permit that enabled the discovery of the new species. José Liétor (Jaén) was helpful in providing specimens of all species in *Iberus* for comparison.

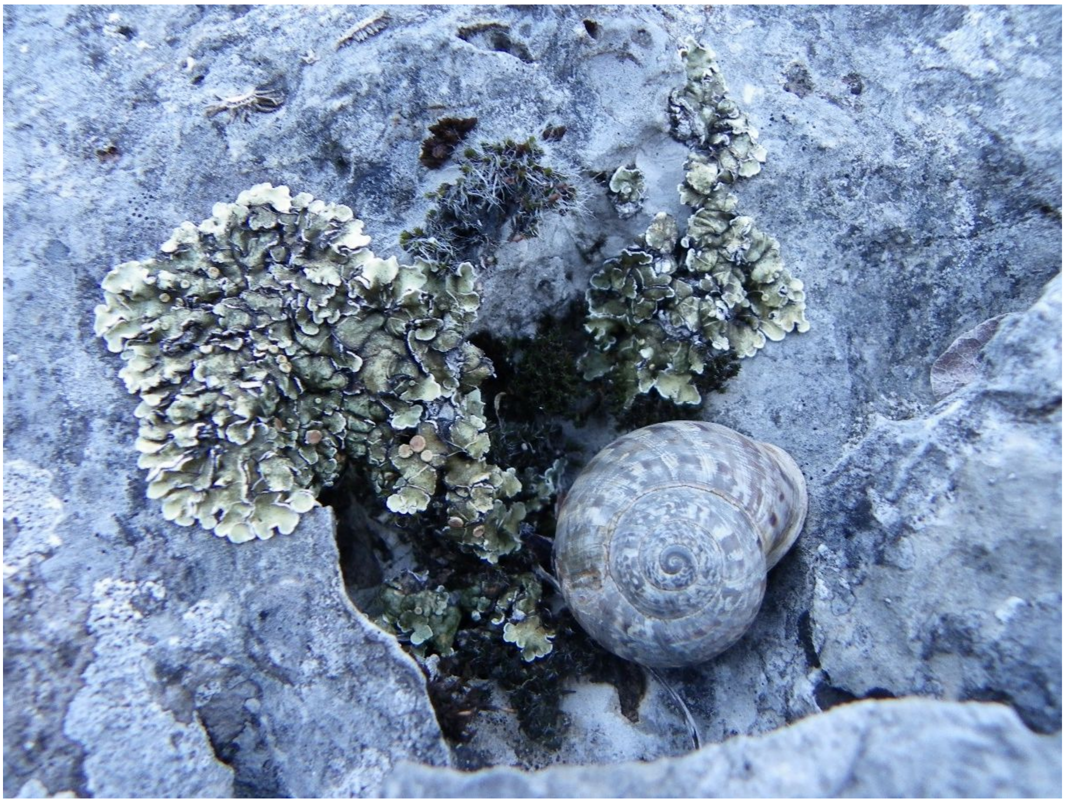

Fig. 7. Live specimen of *Tartessiberus cilbanus* resting inside a crevice with lichens.

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